Review of Palaeobotany and Palynology, 56 (1988): 151–176
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

PALEOECOLOGY OF THE MIDDLE PENNSYLVANIAN-AGE HERRIN COAL SWAMP (ILLINOIS) NEAR A CONTEMPORANEOUS RIVER SYSTEM, THE WALSHVILLE PALEOCHANNEL

WILLIAM A. DIMICHELE and TOM L. PHILLIPS

Department of Paleobiology, (NMNH) Smithsonian Institution, Washington, DC 20560 (U.S.A.)
Department of Plant Biology, University of Illinois, Urbana, IL 61801 (U.S.A.)

(Received January 22, 1987; revised and accepted September 24, 1987)

Abstract

DiMichele, W.A. and Phillips, T.L., 1988. Paleoecology of the Middle Pennsylvanian-age Herrin Coal swamp (Illinois) near a contemporaneous river system, the Walshville paleochannel. Rev. Palaeobot. Palynol., 56: 151–176.

Coal-ball peats were sampled quantitatively in seven profiles from the Old Ben Coal Company No.24 Mine in southern Illinois. The coal and the coal-ball peats are thicker in this near-channel area than at any site sampled so far. Lycopods dominate the peat-swamp flora, as at other Herrin Coal sites, with *Lepidophloios hallii* being the most important (30–78% of whole-profile peat biomass). Ferns (5–15% biomass), and pteridosperms (1–15% biomass), also are important in the swamp flora. Shoot-root ratios in profiles are relatively high, 1.4–2.8. Fusain abundance is concentrated in several mid-seam zones (above the blue-band clastic parting) with the highest pteridosperm abundances.

Three major plant associations ("communities") are detected by multivariate analyses. The most common assemblage is dominated by *Lepidophloios hallii* (>70% of biomass), with low-diversity and little representation of ground-cover and free-sporing plants; this is interpreted as representative of standing-water, high abiotic-stress conditions. *Lepidophloios* assemblages are common in all profiles. *Diaphorodendron scleroticum* and *D. dicentricum* characterize a second assemblage (>20% of biomass) that can include a diversity of species and growth forms; these associations appear to be structured by disturbance. *Diaphorodendron* is most abundant just above the seat earth and in several consecutive zones near the top of the seam. *Medullosa* (>20% biomass) characterizes the third major assemblage; *Medullosa* assemblages are most common at the base of the seam, in proximity to the blue-band clastic parting, and in a mid-seam interval of "dirty" coal. The association of *Medullosa* with zones of >10% fusain and abundant mineral matter suggests alternation of flooded and dry conditions. *Psaronius* tree ferns form an overprint on these distributions, occurring widely in all but *Lepidophloios*-dominated assemblages.

Introduction

Ecological studies of Pennsylvanian-age coal-swamp vegetation provide the environmental and botanical context for peat-to-coal studies as well as the basis for dynamic interpretations of plant biology, including evolution. As the plants and vegetation of coal swamps have become better known, the potential for ecological analyses also has improved markedly. The Herrin Coal Member of the Illinois Basin coal field has been the source of much of our understanding of the biology of Middle Pennsylvanian-age coal-swamp plants, through studies of coalified peat stages in coal balls and coal palynology (Schopf, 1938, 1939; Winslow, 1959; Peppers, 1970; Phillips et al., 1977; Phillips and DiMichele, 1981; Mahaffy,

0034-6667/88/$03.50

1985; Winston, 1986a). The Herrin coal swamp constitutes one of a few large Pennsylvanian ecosystems that can be studied regionally with both coal-ball peat deposits and palynology. Its flora is diverse and drawn from virtually all of the major evolutionary lineages of lowland tropical plants of the time (lycopods, ferns, sphenopsids, pteridosperms and cordaites). The long stratigraphic ranges of many of these plants and their broad distributions permit application of paleoecological interpretations over a wide paleogeographic area and throughout much of Middle Pennsylvanian. This broad data base allows examination of vegetational patterns in detail and assessments of their environmental implications. These data also permit quantitative comparisons with coal palynology and with aspects of coal quality.

The vegetation of the Herrin coal swamp at sites in the Old Ben No.24 Mine is of particular interest because the coal is thick and has extensive, thick, occurrences of coal balls (up to 4 m) containing coalified, anatomically-preserved peat-like plant material (coal-ball peat). The coal balls in this mine are much closer (11.5 km or 7 miles) to a penecontemporaneous active channel, the Walshville paleochannel, than others previously studied in detail. This permits assessment of the effects of such a major geomorphic feature on plant distribution. For example, regional coal-spore floras indicate that *Lycospora*-producing lycopods increase in abundance near the Walshville (Phillips and Peppers, 1984). This pattern also is detected in marginal areas of other coal bodies (Eble et al., 1985; Esterle and Ferm, 1986). Parallel studies in the Old Ben Mine include a local and regional analysis of the geology, including depositional environments (Bauer and DeMaris, 1982), origin and distribution of coal balls (DeMaris et al., 1983), and coal petrology (Johnson, 1979; Harvey and Dillon, 1985).

The Old Ben vegetation is more strongly dominated by lycopod trees (especially *Lepidophloios*) and is less diverse than that from Herrin Coal sites more distant from the Walshville (Phillips et al., 1977; Phillips and DiMichele, 1981). Quantitative differences among profiles of the Old Ben mine suggest some patchiness, but, in general, the vegetation is similar to that of other Herrin study sites. The thickness of peat profiles results from greater repetition of *Lepidophloios*-dominated forests than at most other sites in the Herrin. The most complete profile sequence (VS 3-5), which extends from the underclay to the roof, aids further in the delineation of some lycopod, seed fern and tree fern rise-decline patterns known from other sites in the Herrin Coal, and in the recognition of the main kinds of coal-swamp assemblages ("communities").

Geological setting

The Old Ben No.24 underground mine is located just west of Benton, Illinois in Franklin County with the shaft in the 15′ Ina Quadrangle, Sec.11, T6S, R2E (Fig.1), 11.5 km east of the Walshville paleochannel. The Walshville appears to have flooded the swamp periodically, indicated by intertonguing splits of coal and siltstone, by the low-seam blue band, and by the terminal, non-marine Energy Shale Member, that overlies the coal along the channel. Bauer and DeMaris (1982) and DeMaris et al. (1983) document a terminal sequence of depositional events brought on by marine transgression: choking of the Walshville channel accompanied by major overbank floods and deposition of Energy Shale lobes; erosion of tidal channels into the Energy Shale and peat surfaces, during which old flood channels were reused and new ones created; a transition to restricted marine (Anna Shale Member) and, ultimately, open marine (Brereton Limestone Member) deposits.

Materials

Seven partial profiles of coal-ball peats were collected from the locations shown in Fig.2. These profiles were clustered in two areas of the mine separated by 600 m (Fig.2): VS 1, 2 and 4 in the east and VS 3, 5, 6 and 7 in the west. The major profiles (VS 3–5 and VS 4) were

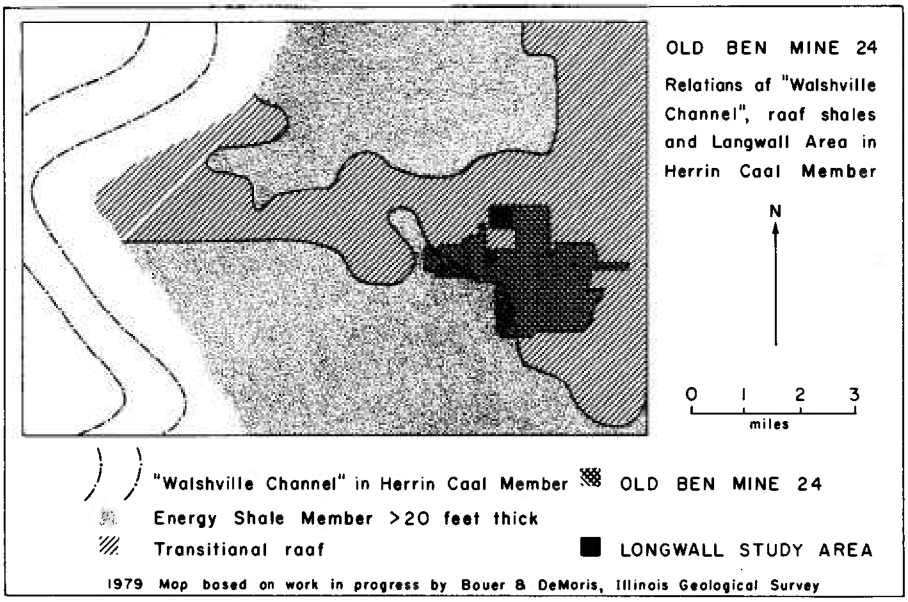

Fig.1. Old Ben Mine 24 in relation to Walshville paleochannel and local roof-shale lithologies.

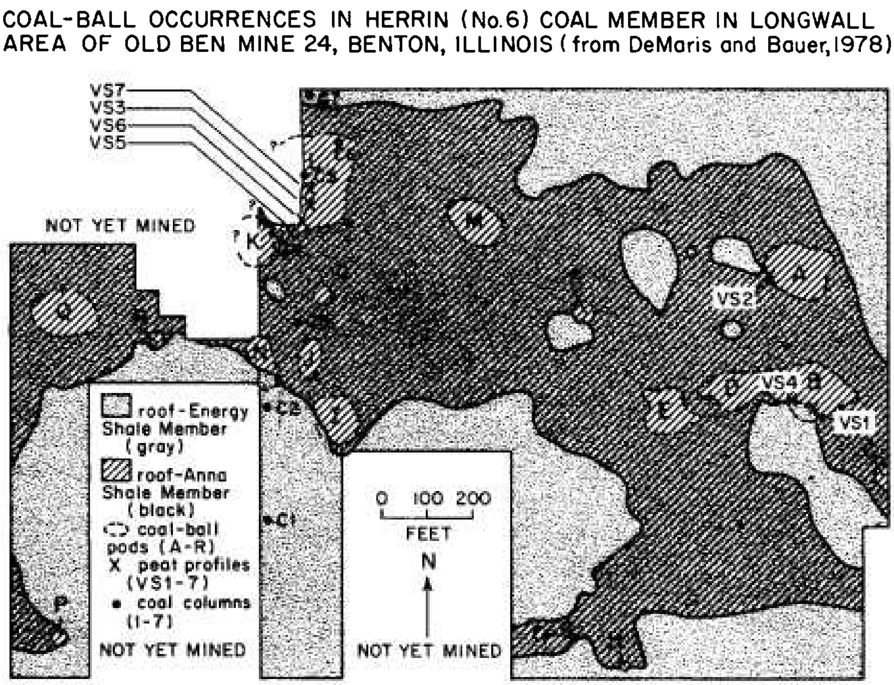

Fig.2. Location of coal-ball pods and coal-ball peat profiles in the Old Ben No.24 Mine.

subject to detailed analysis. All profiles except VS 5 and one zone from VS 7 were from above the blue-band clastic parting (Fig.3). The composition of the profiles was quantified from a total of 634 coal balls with a total surface area of 28,236 cm^2 (information units). Of this total, VS 3 and VS 5 contained 325 coal balls, 29 zones and 16,238 cm^2; they represent

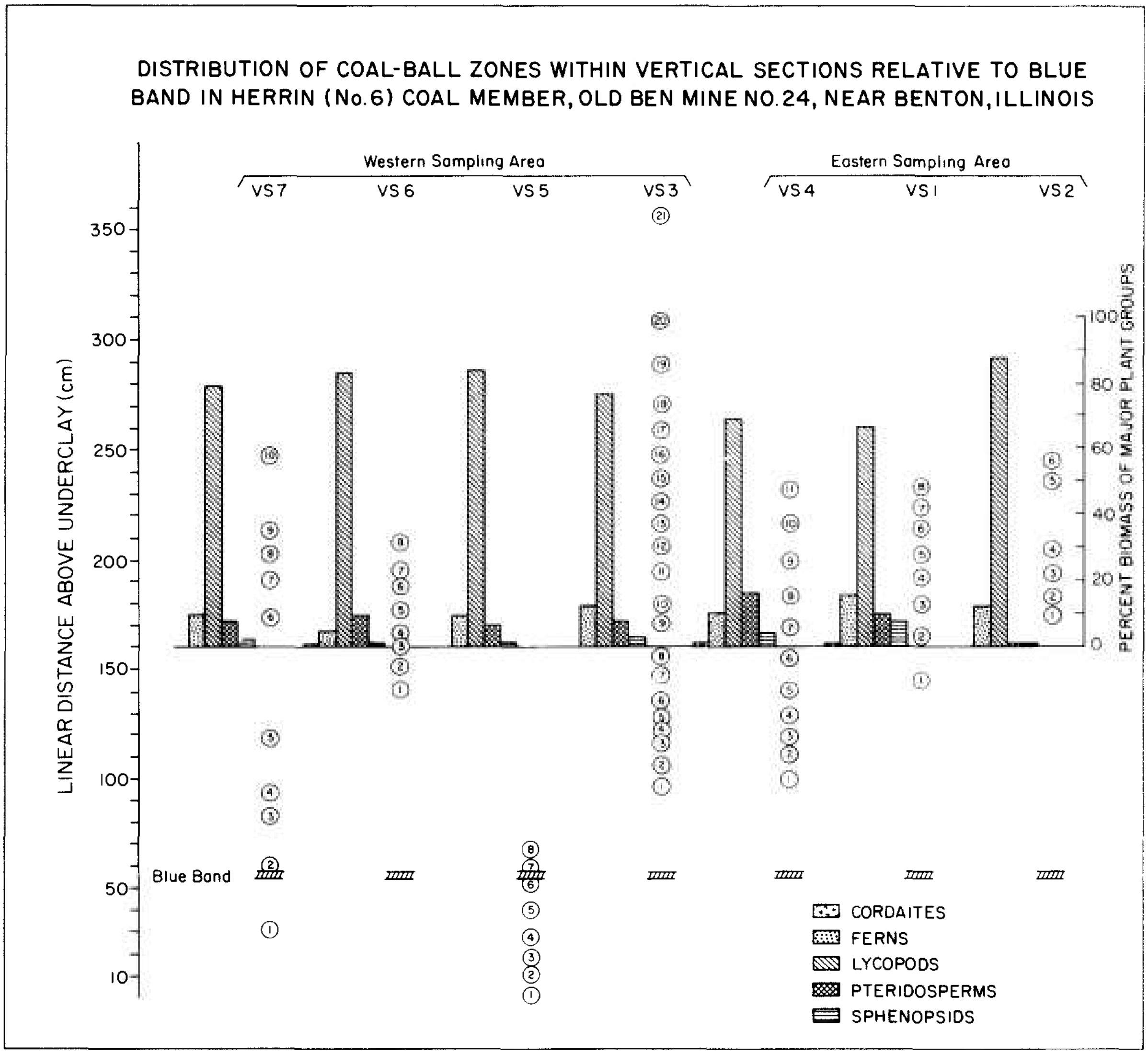

Fig.3. Distribution of coal-ball zones within the seven profiles collected in the Old Ben No.24 Mine. Blue-band clastic parting is the datum. Plant composition (major groups) of the whole profile is indicated by the histogram to the right of the zones.

248.5 cm of the 360 cm seam thickness. A 30-cm thick coal-ball zone was not collected because of roof conditions. Profile VS 4 contained 101 coal balls, 11 zones and 4790 cm^2; this represented 101 cm of the 254-cm seam thickness above the blue band. Collections bear the numbers: 17477–17512, 18702–18802, 19460–19607, 20000–20316, 22344–22478, and 22597–22604. Figure 3 compares the thicknesses of the profiles, number of zones and whole-profile taxonomic composition according to major plant groups. All specimens and peels are housed in the Paleobotanical Collections, Department of Plant Biology, University of Illinois, Urbana, Illinois.

Methods of analysis

Procedures for collection of sequential zones of coal balls in a profile are those of Phillips et al. (1977). Relative percent volume, a measure of biomass, is calculated and analyzed for taxa, organs/tissues, and preservational states (fusain, pyrite) according to the techniques of Phillips and DiMichele (1981). These calculations are made for zones, the basic sampling units in the profile, and on a whole profile basis.

There are three data sets: *whole-peat* data including the category unidentified, *normalized* 100% identified data, and *root-free* data derived from tabulation of aerial organs and tissues from which both unidentified and root material have been deleted. Abundances of fusain and unidentified material (often fusinized) are obtained from whole-peat data. Normalized data are used to compile the abundance of taxonomic groups and organs in each zone. Root-free data are used for community analysis. Removal of the root component of the data is necessary because roots may have penetrated the peat at a later time. Because *Psaronius* stems were encased in a mantle of aerial roots, fifty percent of the amount of *Psaronius* outer roots are added back to the aerial composition component as an estimate of the actual aerial root mantle. Because lycopods commonly form 60–80% of the biomass in profiles, histograms are prepared for only the aerial lycopod tissues/organs in each zone, normalized to 100%.

Community analysis techniques

Methods used in community analysis are outlined by Whittaker (1975), Gauch (1982), Greig-Smith (1983) and Pielou (1984). The simplest measures are those that express the degree of taxonomic-floristic similarity among zones of a profile. Beta diversity is a relative measure reflecting the variability within profiles. Sorenson's community coefficient expresses the taxonomic-compositional similarity of any two zones based on the number of taxa the zones have in common, varying from zero (no shared taxa) to 1.00 (identical composition). Beta diversity and community coefficient do not measure quantitative differences between samples.

The quantitative comparison of zones is expressed as a percentage similarity. Relative importance values of taxa (percent volume measures) are criteria for assessing this similarity, which varies from 0.00 to 100.00.

Simultaneous comparison of many profile zones is done by two kinds of ordination methods: Bray-Curtis (polar) indirect ordination, based on percentage similarity, and Detrended Correspondence Analysis (Gauch, 1982). The latter technique provides estimates of the total variation among zones accounted for by each ordination axis (eigenvalues). The patterns detected in our data by the two methods were very similar.

Dominance-diversity curves were prepared for the assemblages of each zone in a profile. The curve displays the distribution of biomass in a zone, which can be considered to be a reflection of the resource partitioning among the constituent plants. Steepness and shape of the curve indicate the relative levels of dominance within the assemblage.

Results

Taxonomic groups

There are five major taxonomic groups, represented predominantly by trees, in coal-ball peats from the Herrin Coal (Table I; Fig.3): lycopods, ferns, pteridosperms, sphenopsids and cordaites, in descending order of importance. Composition of Old Ben 24 profiles by major genera and species is presented in Table II. The ranges of abundance given in this section are based on all seven profiles. In subsequent sections we confine the analysis to VS 3, 4 and 5.

Arborescent lycopods were the major contributors to biomass in all profiles, accounting for 66–86% of the identified biomass. Many lepidodendrid lycopods were large trees, 15–30 m tall (Thomas and Watson, 1976; Wnuk, 1985), that produced thick bark as the major structural support tissue. Most of the lycopod

TABLE I

Major-group taxonomic composition (normalized basis) of profiles

VS No.	Ferns	Lycopods	Pteridosperms	Sphenopsids	Cordaites
3	12.59	76.83	7.59	2.89	0.09
4	10.12	68.94	16.28	4.09	0.54
5	8.95	83.80	6.22	1.50	0.04
1/2 and 6/7	5.17–15.67	66.60–86.09	0.92–10.19	0.80–6.86	0.00–0.67

TABLE II

Comparative taxonomic composition (root-free basis): profiles VS 1-7[a]

	Western area				Eastern area		
	Blue band above mid-seam and below blue band			Blue band to mid-seam	Mid-seam	Mid-seam	Mid-seam
	VS 5	VS 3	VS 6	VS 7	VS 4	VS 1	VS 2
Lepidophloios hallii	65.1	55.6	77.4	61.9	29.6	47.0	29.5
Diaphorodendron dicentricum	0.2	7.6	6.4	11.8	13.3	9.4	5.0
Diaphorodendron scleroticum	1.5	7.1	1.3	0.0	7.6	0.0	42.4
Paralycopodites brevifolius	15.4	0.5	0.0	0.1	0.0	0.0	2.1
Sigillaria spp.	0.0	0.6	0.0	3.6	2.6	9.2	6.3
Total lycopods	82.2	71.4	85.1	77.4	53.1	65.6	85.3
Psaronius	8.5	12.1	5.1	9.5	9.8	14.9	12.0
Arthropitys	1.1	2.0	0.9	2.1	3.8	6.5	0.5
Sphenophyllum	0.4	0.9	0.5	0.5	0.3	0.4	0.3
Medullosa	5.5	5.6	8.6	7.2	15.6	8.1	0.8
Callistophyton	0.6	1.0	0.4	0.4	0.6	1.6	0.1
Cordaites	0.1	0.1	0.6	0.0	0.5	0.7	0.0
% Unidentified	4.6	9.5	9.0	14.8	10.9	4.1	2.0

[a]Not all taxa are included. Unidentified determined separately from whole-peat data set, shown here for comparison.

tissues are bark and cortical tissues from stems, and parenchymatous rootlets of stigmarian root systems (Table III).

The most abundant of the lycopods is *Lepidophloios hallii* (29–77%; Table II). Others include *Diaphorodendron scleroticum*, *D. dicentricum* (see DiMichele, 1985, for discussion of the name *Diaphorodendron*), *Paralycopodites brevifolius* and *Sigillaria*. Histograms of relative lycopod abundance (normalized to 100% lycopod aerial portions) in profiles VS 3–5 (Fig.4) illustrate the following patterns: very abundant *Diaphorodendron scleroticum* in the basalmost zone, *Paralycopodites* alternating with *Lepidophloios* up to just above the blue band, and *Lepidophloios* as the main lycopod in all but a few of the subsequent zones. Distinctive exceptions to the importance of *Lepidophloios* above the blue band are *Sigillaria*-rich zone 11, a suite of zones with very abundant *Diaphorodendron* (zones 24–27), and two zones with a diversity of lycopod taxa (zones 13 and 29). On a root-free basis, *Lepidophloios* dominates practically all of the zones in which lycopod biomass is 50% or more; the exception is the abundance of *Paralycopodites* in

TABLE III

Organ composition of profiles (normalized basis) by major plant group

	Fructifications	Leaves	Stems	Total aerial	Roots	Shoot/root ratio
VS 1						
CR	0.0	0.0	0.68	0.0	0.0	
FE	5.09	4.31	1.57	10.97	4.70	
LY	4.50	2.94	42.51	49.95	16.65	
PT	0.78	8.13	1.18	10.09	0.10	
SP	0.29	0.0	1.96	2.26	4.60	
Totals	10.66	15.38	46.33	72.38	26.05	2.78
VS 2						
CR	0.0	0.0	0.0	0.0	0.0	
FE	4.02	1.09	0.0	5.11	7.06	
LY	2.99	1.26	55.40	59.65	26.44	
PT	0.17	0.75	0.0	0.92	0.0	
SP	0.06	0.0	0.34	0.40	0.40	
Totals	7.24	3.10	55.74	66.08	33.90	1.95
VS 3						
CR	0.0	0.0	0.09	0.09	0.0	
FE	1.61	1.92	0.07	3.60	8.98	
LY	1.67	3.95	42.34	47.96	28.87	
PT	0.54	5.96	0.89	7.39	0.20	
SP	0.11	0.17	2.17	2.45	0.44	
Totals	3.93	12.00	45.56	61.69	38.49	1.60
VS 4						
CR	0.02	0.0	0.52	0.54	0.0	
FE	0.77	1.10	0.21	2.08	8.03	
LY	2.75	5.28	34.84	42.89	26.06	
PT	0.40	15.13	0.70	16.23	0.05	
SP	0.02	0.02	3.62	3.66	0.42	
Totals	3.96	21.53	39.91	65.40	34.55	1.89
VS 5						
CR	0.0	0.0	0.04	0.04	0.0	
FE	1.32	1.93	0.0	3.25	5.70	
LY	2.06	1.32	53.88	57.62	26.04	
PT	0.31	5.52	0.39	6.22	0.0	
SP	0.31	0.0	0.66	0.97	0.53	
Totals	4.00	8.77	54.94	67.74	32.27	2.10
VS 6						
CR	0.0	0.0	0.04	0.04	0.0	
FE	0.85	0.25	0.17	1.27	3.90	
LY	0.85	1.78	42.96	45.59	37.45	
PT	0.55	8.86	0.42	9.83	0.0	
SP	0.04	0.0	0.55	0.59	0.76	
Totals	2.29	10.89	44.65	57.83	42.11	1.37
VS 7						
CR	0.0	0.0	0.0	0.0	0.0	
FE	4.95	1.36	0.0	6.31	3.80	
LY	2.78	2.30	40.95	46.03	33.15	
PT	0.41	7.66	0.0	8.07	0.0	
SP	0.0	0.0	0.75	0.75	1.83	
Totals	8.14	11.32	41.70	61.16	38.78	1.58

CR = Cordaites; FE = Ferns; LY = Lycopods; PT = Pteridosperms; SP = Sphenopsids.

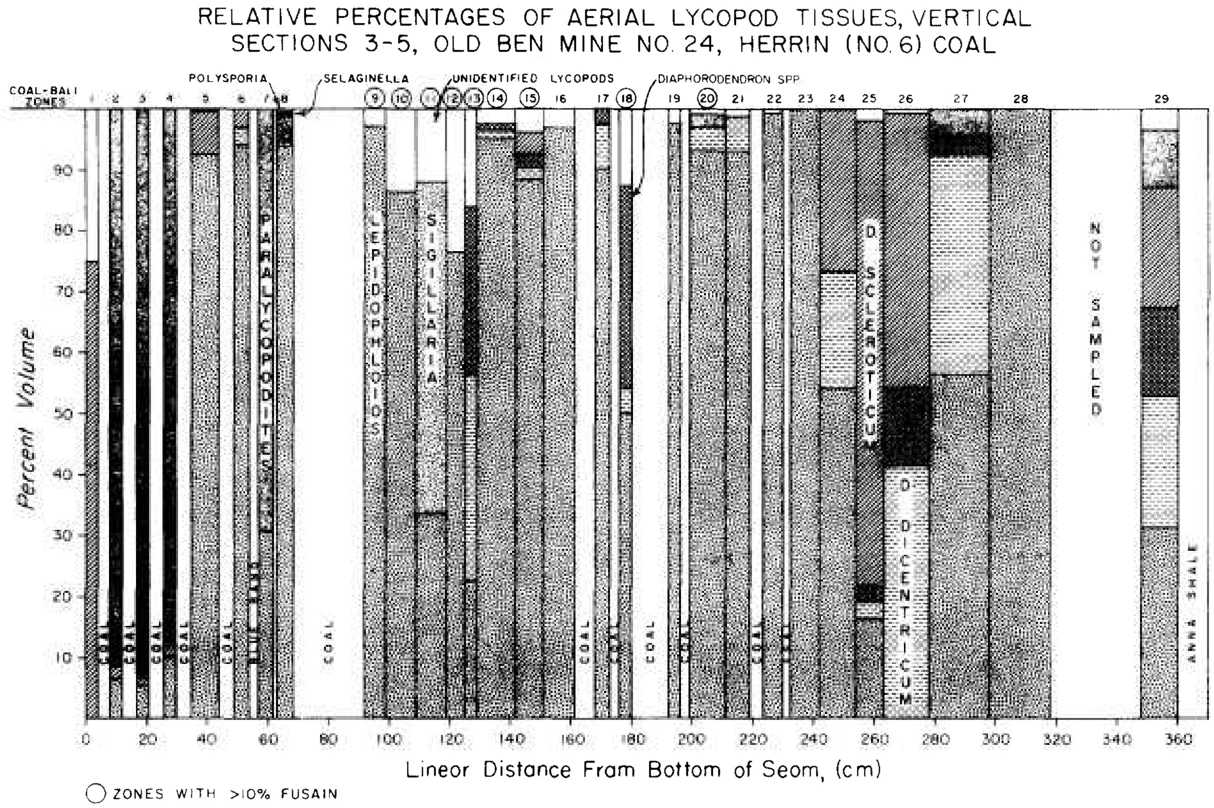

Fig.4. Profile VS 3-5. The taxonomic composition of lycopods in each zone is indicated as a fraction of total aerial-lycopod organs in that zone.

proximity to the blue band. Consequently, most low lycopod-abundance values generally reflect a shift to lycopod trees other than *Lepidophloios* as well as to other plant groups as dominant elements. In general, there is an oscillation of *Lepidophloios* dominance with other assemblages, tree ferns and pteridosperms in particular.

Ferns contribute 5–16% of profile biomass (see Table I). This largely reflects the abundance of *Psaronius* tree ferns (Table II). Most identified stems resemble *P. chasei* Morgan (1959), but do not appear to be conspecific (A. Lesnikowska, pers. comm., 1986). Fertile organs are mostly of the *Scolecopteris minor* or *S. parvifolia* types (Millay, 1979). Although a number of *Scolecopteris* species have been reported from the Herrin coal swamp, few species occur in more than trace amounts, and *S. minor* may be the major species. Coenopterid ferns contribute $< 1\%$ of the biomass.

Pteridosperm abundances are 1–16% (Table I). Medullosans comprise most of this biomass as leaf tissues, a small percentage of stems, and few roots (Table III). Pteridosperms varied in habit from small trees, the most important medullosan forms, to viney climbers or scramblers, of which *Callistophyton* is the most uniformly distributed (Table II).

Medullosan petioles and rachises (*Myeloxylon*) are difficult to differentiate to species, and we rely on ovules and foliage-types to indicate total medullosan diversity, which is three to five species. Identified pteridosperm foliage includes *Alethopteris lesquereuxii* (Baxter and Willhite, 1969), *Alethopteris* sp., *Neuropteris rarinervis* (Oestry-Stidd, 1979), *Neuropteris ?scheuchzeri* (Schabilion and Reihman, 1985), and *Linopteris*, possibly indicative of *Sutcliffia* (Stidd et al., 1975), which is found rarely. The ovules *Pachytesta gigantea* and *P. illinoense* (Taylor, 1965) also have been identified. Of the small pteridosperms, *Callistophyton boysettii* (Rothwell, 1981) is the most common; *Heterangium americanum* (Shadle and Stidd, 1975) occurs rarely in some profile zones and frequently is fusinized.

Sphenopsids make up 1–7% of biomass (Table I). This is mostly stem wood and cortical tissues of *Arthropitys* and, to a much lesser extent, of *Sphenophyllum* (Table II). In some zones calamite root wood (*Astromyelon*) is an important element.

Cordaites account for <1% of biomass (Table II). Most of the tissues are stem wood and cortex. The presence of *Cardiocarpus oviformis* ovules suggests that the predominant stem species is the *Cordaixylon* (*Pennsylvanioxylon*) type (Rothwell and Warner, 1984).

Composition of profiles 3, 4 and 5

Normalized data sets (100% identified) come from the lower part of the seam (VS 5) and the main upper seam (VS 3 and 4). Composition of all profiles is presented in Table III. Total unidentified composition of coal-ball peat is 4.6% in VS 5, and 9.5–10.9% in VS 3 and 4.

Organs and tissues

Aerial, mostly shoot, tissues make up 67.7% of total peat volume in VS 5 and 61.2–65.4% in VS 3 and 4. Lycopod stems account for 34.8–54.9% of total aerial components; pteridosperm leaves comprise 5.5–15.1%. Reproductive organs, largely fern sporangia and lycopod cones, are 3.9–4.0% of the biomass.

Roots account for 32.3–38.5% of the total peat volume. Most roots are from stigmarian root stocks of lycopod trees. Profiles in which *Lepidophloios* is most abundant (VS 3, 5, 6, 7) are also the most heavily rooted by stigmarian axes. The other major root contributor is *Psaronius*. The root wood and rootlets of calamite trees (*Astromyelon*) are a significant component of VS 1.

The general tissue composition of VS 3 (Table IV) is of potential interest for comparisons to petrographic analyses. Of the total biomass 45.9% is parenchyma. Bark, mostly from lycopods, accounts for 36.7%. Wood, mostly from roots and stems of calamites and the central cylinders of stigmarian axes, accounts for only 4.7%.

Parenchyma is derived largely from many

TABLE IV

Tissue composition of VS 3 (whole-peat basis)

Lycopod periderm	33.5% aerial; 2.8% stigmarian
Lycopod wood	0.6% aerial; 1.3% stigmarian
Lycopod cortical tissues	4.1% aerial; 1.4% stigmarian
Lycopod stems	2.8% (mostly cortical tissues and periderm)
Stigmarian rootlets	22.3% (mostly cortical tissues)
Psaronius roots	8.5% (mostly cortical tissues)
Sphenopsid wood	1.9% aerial and root combined
Sphenopsid stems	0.6% (mostly wood)
Pteridosperm non-woody tissues	6.2%
Unidentified periderm	0.4%
Unidentified wood or secondary tissues	0.9%
Total fructifications	4.4%
Total cortical tissue (parenchyma)	45.9% (30.8% roots)
Total periderm	36.7%
Total wood and woody organs	4.7%
	91.7% of total normalized peat volume

small organs. It often is partially degraded or dispersed throughout the peat. The largest source is stigmarian rootlets, which constitute 30.8% of total biomass. Pteridosperm cortical parenchyma, frequently with sclerenchyma and secretory inclusions, is locally abundant.

Lycopod bark (periderm) sheets comprise 33.5% of the total biomass in VS 3. Most of this periderm is the homogeneous, resinous, and decay-resistant *Lepidophloios*-type; this is often the only recognizable tissue in highly degraded coal-ball peats. Phellem (outer bark) from *Diaphorodendron* is histologically similar to *Lepidophloios* periderm and also occurs in extensive sheets. *Diaphorodendron* phelloderm (inner bark) is porous and more degraded than the thinner phellem.

Fusain

Fusain varies in the profiles from 1.6 to 11.8%, averaging 6.6% of the whole-peat volume (Table V). Fusain is most abundant in coal-ball zones from the mid-portion of the seam. Profiles 3 and 4 contain 11.8% and 8.1% respectively. Profile 5, at and below the blue band, contains only 4.9%. On average, 2.9% of whole-profile peat volume is lycopod-derived fusain. Unidentified fusinized tissues average 2.2%, and pteridosperms contribute 1.1%.

The coal-ball peat of pteridosperms and sphenopsids is fusinized disproportionately more than other groups: 11.0% and 6.5% respectively, whereas lycopods average 4.3% and ferns, 2.8%. This suggests that certain growth habits or habitats were more conducive to such a preservational state (Table V). Unidentified material accounts for a relatively small amount of total biomass; however, 23.9% of unidentified material is fusinized (Table V). This, in part, reflects the biases resulting from fusinized preservation, which variously pre-

TABLE V

Fusain abundance by profile and taxonomic group (whole-peat basis)

	Percent of total profile fusain						
	Unidentified	Ferns	Lycopods	Pteridosperms	Sphenopsids	Cordaites	Total
Eastern profiles							
VS 1	1.98	0.38	5.44	1.97	0.19	0.0	9.96
VS 2	0.22	0.17	1.13	0.0	0.11	0.0	1.63
VS 4	2.57	0.20	2.21	3.08	0.08	0.0	8.14
Western profiles							
VS 3	2.41	0.76	7.28	0.99	0.28	0.05	11.77
VS 5	2.08	0.06	0.18	0.36	0.0	0.0	2.68
VS 6	1.73	0.12	1.85	1.12	0.12	0.0	4.94
VS 7	4.14	0.29	2.23	0.23	0.12	0.0	7.01

	Percent of each group fusinized					
	Unidentified	Ferns	Lycopods	Pteridosperms	Sphenopsids	Cordaites
Eastern profiles						
VS 1	48.06	2.53	8.53	20.00	2.89	0.0
VS 2	11.11	1.41	1.33	0.0	14.28	0.0
VS 4	23.62	2.22	3.60	21.21	2.20	0.0
Western profiles						
VS 3	25.29	6.67	10.48	14.28	10.69	62.50
VS 5	12.05	0.76	0.27	5.77	0.0	0.0
VS 6	19.26	2.55	2.45	12.27	9.76	0.0
VS 7	27.91	3.37	3.30	3.32	5.48	0.0
Average	23.90	2.79	4.28	10.98	6.47	

serves cellular detail but may render the material unidentifiable to a taxonomic group.

Root–shoot patterns

The shoot–root ratio of VS 5 is 2.1 and those of VS 3 and 4 are 1.6 and 1.9, respectively. These are moderately high ratios compared to other Pennsylvanian-age coals (Phillips et al., 1985), generally indicative of relatively good preservational conditions. Nevertheless, such ratios suggest that 50–90% of the original peat was not preserved (Phillips et al., 1977). There are two biasing factors in calculating shoot–root ratios. In some zones the shoot–root ratio is biased upward by differential decay of most tissues except lycopod periderm. In others, roots, which would compress more during compaction of the coal than many other tissues, may be little compressed in coal-ball peats, lowering the shoot–root ratio.

Community analyses

Profile patterns

Distribution of plant assemblages in the two main profiles, VS 3–5 and VS 4, is illustrated for the major plant groups based on whole-peat data in Figs.5 and 7, and for the important genera and/or species based on root-free data in Figs.6 and 8.

Lepidophloios hallii is present in almost every zone and accounts for most of the major peaks of lycopod abundance in profiles. *Diaphorodendron scleroticum* is irregular in distribution, occurs most often in several consecutive zones and occasionally accounts for a large percentage of lycopod biomass. *Diaphorodendron dicentricum* is widely distributed, occurring in 30 of the 40 zones sampled, but generally its root-free abundances are less than 20%. *Paralycopodites* occurs only in VS 3–5 where its greatest abundances, as the dominant lycopod of the assemblage, are in the lower part of the seam. *Sigillaria* is rare in most profiles but, where it does occur, it is often a significant or dominant element of the flora.

Medullosan pteridosperms are irregularly abundant in profiles. Zones of elevated abundances usually correspond to declines in lycopods, particularly *Lepidophloios hallii*. All other arborescent lycopods may rise in abundance along with *Medullosa*, and even show abundance levels comparable to those of *Medullosa*. *Psaronius* tree ferns occur in all but one zone of VS 3–5 and VS 4. As with *Medullosa*, the higher abundances of *Psaronius* correspond to sharp decreases in *Lepidophloios hallii*. However, *Psaronius* and *Medullosa* do not mirror each other consistently throughout the profiles. Sphenopsids and cordaites are much less abundant than the other groups and show few distinct patterns at the level of profiles.

Spatial patterns

Analyses of the floristic relationships among the zones of a profile relies, in essence, on elimination of the time element. All zones are treated as if they coexisted, creating a more manageable spatial gradient-analysis problem. The lack of a whole-seam succession, and the general qualitative similarity of assemblages within and among profiles, indicate that evolutionary time was not a biasing influence on vegetational change in the Herrin Coal. Thus, treating the zone assemblages as coexistent and as reflecting intraswamp gradients seems valid.

In VS 3, 5, 6, and 7 from the western sampling area (Figs.3 and 4), abundances of *Lepidophloios hallii* are moderate to very high in some zones. In contrast, VS 1, 2, and 4 from the eastern sampling area, are more heterogeneous, have fewer zones of high *L. hallii* abundance, and a large number of zones with moderate levels of *L. hallii*.

Beta diversity in VS 3–5 is 3.5 (25 taxa in the profile with average of 7.3 taxa per zone). Fifty-nine percent of the community coefficient comparisons made in VS 3–5 (Fig.9; Table VI) are >0.67, indicating that most of the zones are similar in taxonomic composition. The variability in the profile is due largely to variation in the quantitative composition of the zones and to a few diverse zones with uncommon species (e.g., zone 29), rather than differences in basic floristics. In contrast, the beta

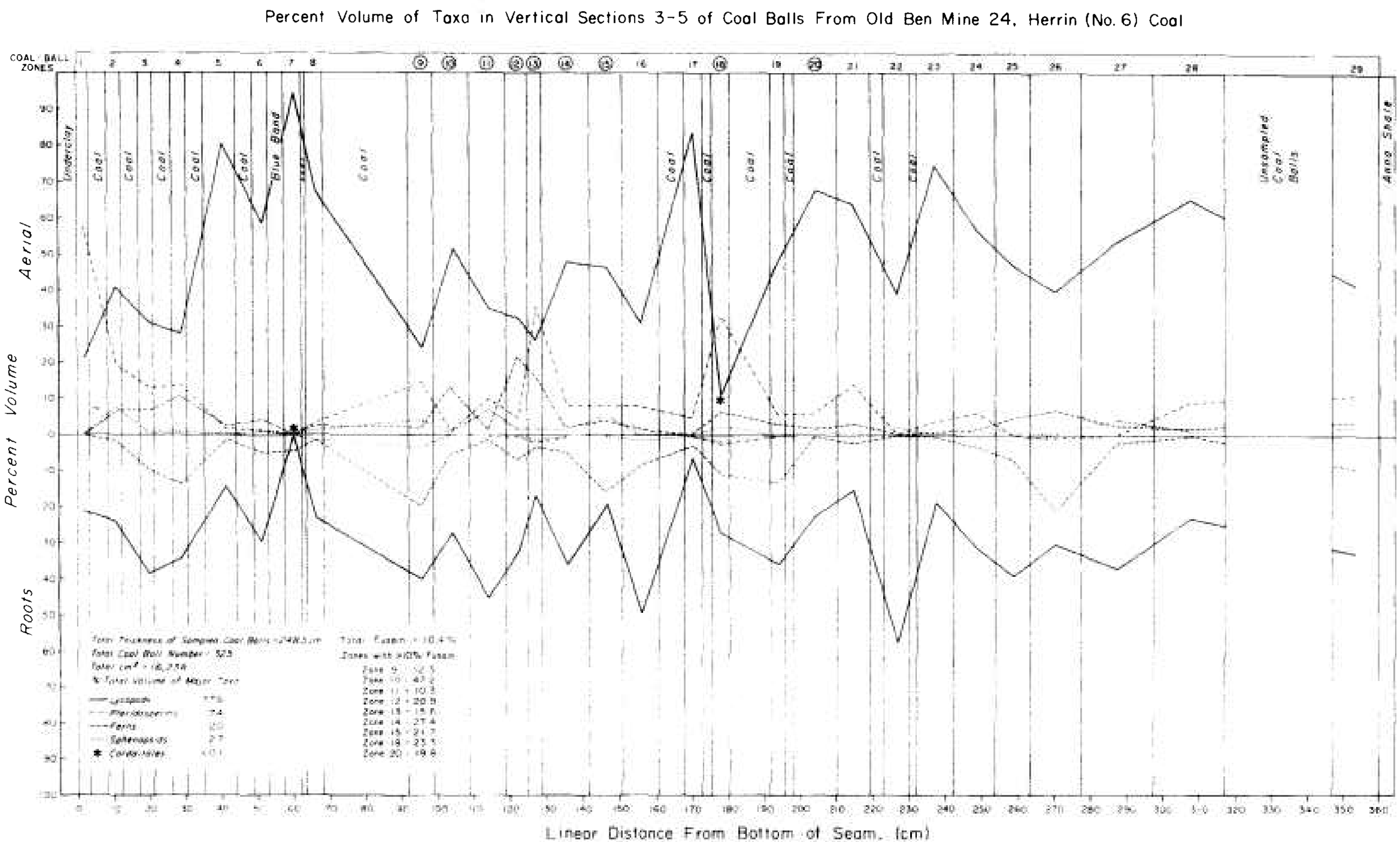

Fig.5. Profile VS 3-5. Percent volume of shoot and root tissues of major groups (lycopods, ferns, pteridosperms, sphenopsids, and cordaites) by coal-ball zone, based on normalized data.

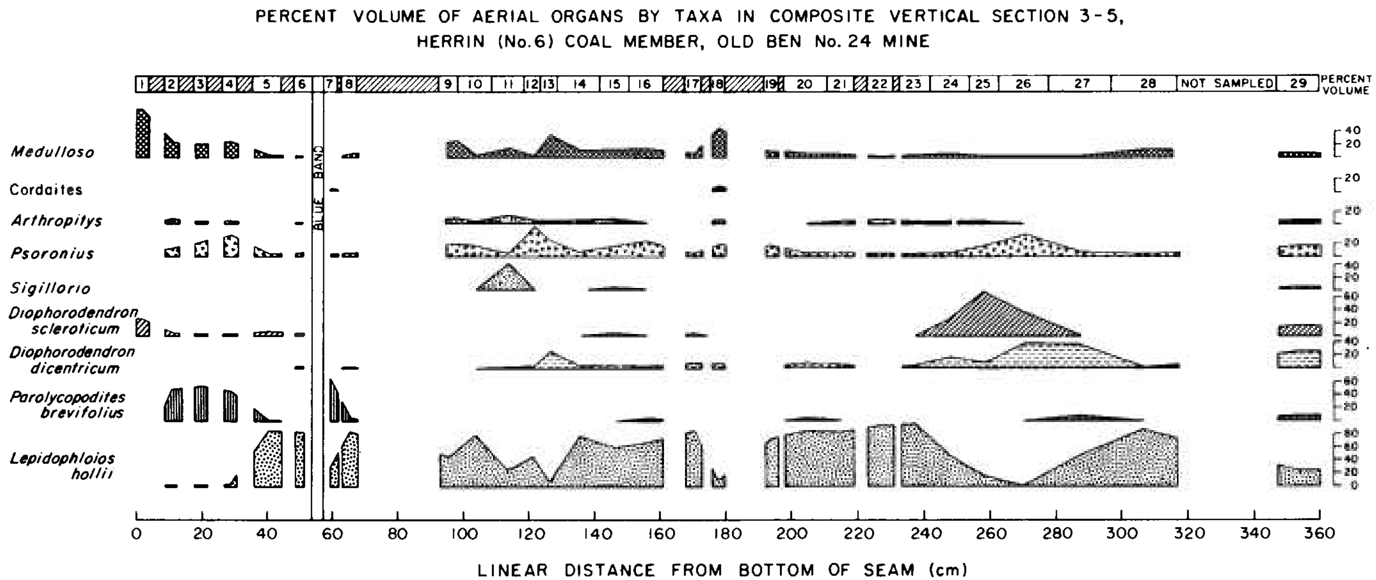

Fig.6. Profile VS 3-5. Percent volume of aerial tissues of major taxa by coal-ball zone, based on root-free data.

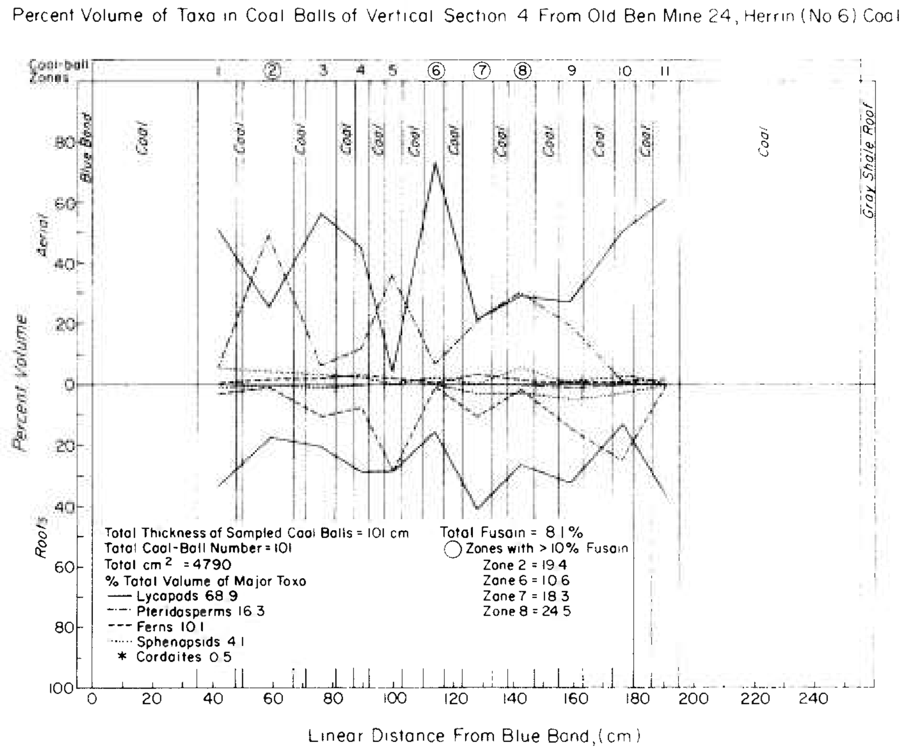

Fig.7. Profile VS 4. Percent volume of shoot and root tissues of major groups (lycopods, ferns, pteridosperms, sphenopsids and cordaites) by coal-ball zone, based on normalized data.

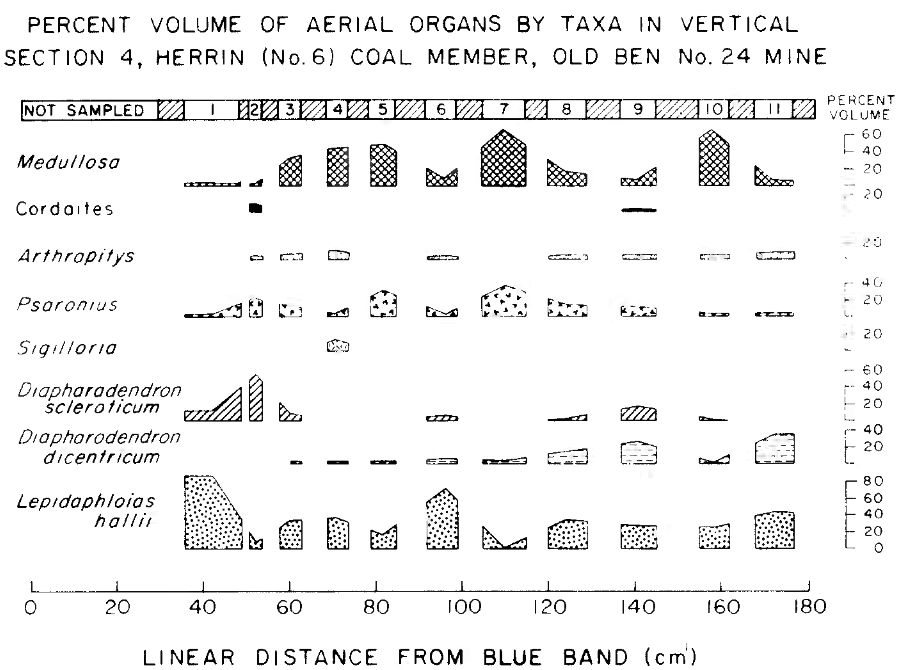

Fig.8. Profile VS 4. Percent volume of aerial tissues of major taxa by coal-ball zone, based on root-free data.

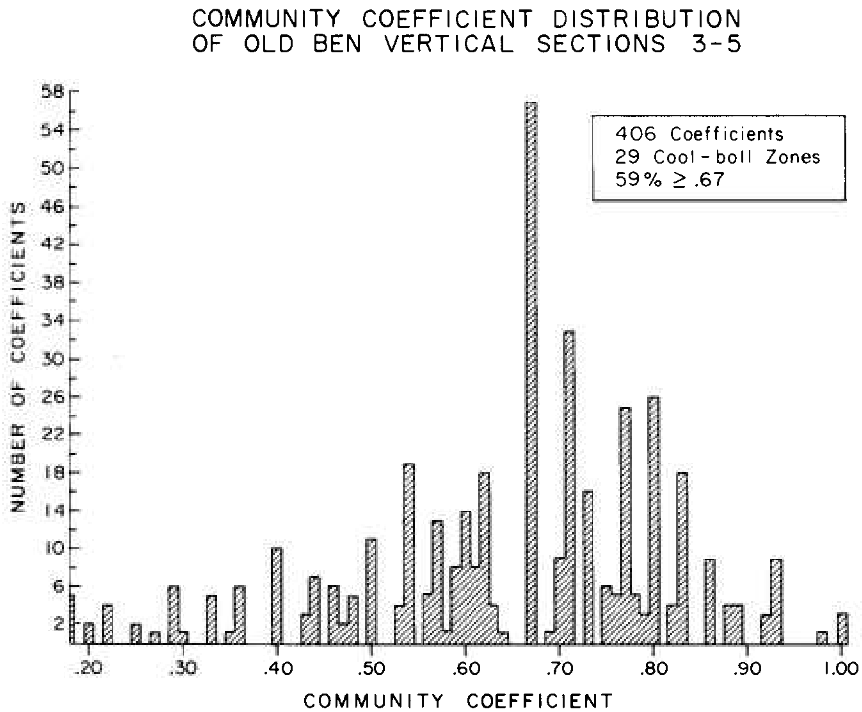

Fig.9. Frequency distribution of community coefficients derived from pair-wise comparison of all zones in VS 3-5, based on root-free data.

diversity of VS 4 is 2.5 (18 taxa in the profile with an average of 7.3 taxa per zone). Although the average number of taxa per zone is the same in VS 3–5 and VS 4, the lower beta diversity of VS 4 is due to fewer species in the profile. This is apparently the result of sampling a narrower interval of the seam and the consequent smaller sampling base. Community coefficients in VS 4 (Table VII), as in VS 3–5, indicate similarity among zones; the distribution is narrower in VS 4, and only 43% of the coefficients are >0.67, suggesting greater compositional heterogeneity among zones in the profile, despite having fewer total species.

(1) Ordinations. Similar assemblages appear in polar ordinations of VS 3–5 and VS 4 (Figs.10 and 11). In the ordination of VS 3–5, zones 1 and 7 were eliminated because of small sample size. All 11 zones were used in the polar ordination of VS 4. End point choices in these indirect ordinations were made on the basis of relative zone dissimilarities (Tables VI and VII), in accordance with the techniques of Bray-Curtis ordination.

Three basic assemblages are revealed by the ordinations. These are characterized by 70–75% *Lepidophloios*, 20–30% *Medullosa*, and 20–70% *Diaphorodendron*, with little or no overlap in the ordination. An intermediate "region" in both VS 3–5 and VS 4 is characterized by 30–70% *Lepidophloios*. In VS 3–5 more zones are compositionally intermediate than in VS 4. However, in both profiles the assemblages with 30–70% *Lepidophloios* overlap with those in which *Medullosa* or *Diaphorodendron* are the major elements.

Psaronius, represented largely by the *Scolecopteris minor*-producing species, does not fall within a narrowly circumscribed "region" of the ordination. Zones with up to 10% *Psaronius* biomass are rich in *Medullosa* and/or *Diaphorodendron* or they are transitional *Lepidophloios* zones. *Psaronius* abundances are very low in zones where *Lepidophloios* exceeds 70–75%.

TABLE VI

Matrix of percentage similarity and community coefficients for plant assemblages in coal-ball zones of Old Ben vertical section 3 5, in the Herrin (No.6) Coal

OLD BEN COMPOSITE VERTICAL SECTION 3-5

COAL-BALL ZONES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1.	-	24.7	20.3	23.6	9.0	1.2	0	4.1	26.3	1.1	14.5	1.5	32.1	10.7	13.4	12.1	5.2	45.4	9.7	7.5	7.7	1.0	4.6	29.7	27.0	26.9	0.4	12.1	20.6
2.	.40	-	87.0	77.9	10.9	15.8	55.2	16.5	45.5	16.9	33.2	21.1	42.1	25.1	34.6	27.4	12.4	44.3	24.8	17.1	18.0	11.9	10.2	19.6	17.8	12.5	14.9	18.2	35.7
3.	.44	.93	-	84.1	9.9	15.0	57.2	14.9	43.8	24.1	24.6	29.3	47.2	23.2	32.8	37.4	11.5	44.2	30.6	15.5	16.7	6.9	9.5	18.0	20.3	21.8	13.3	16.6	37.0
4.	.44	.95	1.00	-	12.3	17.1	44.2	17.1	49.4	26.3	27.3	41.3	53.0	25.9	35.8	39.8	13.6	49.2	32.7	17.7	18.9	9.6	11.7	19.7	22.8	32.1	15.5	18.8	39.2
5.	.57	.77	.83	.83	-	88.3	32.2	91.5	52.0	83.9	30.0	49.8	14.4	81.7	66.3	71.0	88.5	15.3	78.2	87.7	86.9	88.9	90.6	58.3	24.7	10.4	52.9	89.0	34.7
6.	.40	.88	.80	.80	.62	-	31.7	88.3	56.2	89.6	31.3	56.9	24.8	86.5	72.9	76.2	92.4	25.7	82.7	90.3	90.8	85.9	86.1	57.9	28.1	15.1	59.7	85.8	38.5
7.	0	.50	.54	.54	.67	.33	-	36.2	31.8	31.8	26.3	31.6	10.8	31.8	31.8	31.8	31.7	13.1	31.8	33.4	31.8	30.6	30.9	31.9	15.9	2.2	35.0	31.0	31.2
8.	.18	.59	.50	.50	.57	.58	.46	-	53.6	83.6	33.7	51.5	18.2	83.7	68.4	73.[illegible]	90.6	18.1	80.0	92.1	89.9	87.7	91.0	54.3	19.4	4.7	58.5	19.0	34.7
9.	.33	.67	.73	.73	.67	.67	.50	.46	-	66.5	50.7	67.8	55.6	66.8	79.3	77.9	52.9	57.0	72.9	56.1	58.9	53.9	52.6	57.4	30.2	20.0	52.[illegible]	59.6	47.8
10.	.29	.77	.83	.83	.60	.77	.44	.43	.89	-	31.1	65.6	29.3	85.7	77.2	84.8	82.8	29.6	90.9	83.4	35.9	52.1	82.2	52.4	30.[illegible]	18.6	54.8	81.6	40.1
11.	.17	.67	.59	.59	.40	.79	.29	.53	.57	.67	-	35.0	32.3	43.1	49.2	42.1	32.9	34.5	39.0	36.7	38.4	32.4	31.0	38.1	21.2	5.5	32.2	38.9	41.0
12.	.20	.75	.67	.67	.46	.88	.33	.71	.67	.77	.78	-	41.4	56.9	66.6	69.1	50.5	38.2	64.3	51.6	54.0	49.1	48.5	55.6	32.2	32.6	52.7	48.6	46.1
13.	.22	.80	.71	.71	.50	.93	.36	.63	.73	.83	.82	.93	-	30.1	41.9	43.7	24.8	73.0	36.4	24.4	26.2	12.0	15.4	39.9	29.9	46.0	39.8	23.4	58.2
14.	.22	.67	.71	.71	.50	.80	.36	.50	.73	.83	.82	.80	.86	-	81.8	84.3	85.1	32.8	89.7	88.4	91.1	80.9	82.4	60.0	24.3	9.4	56.6	87.7	42.2
15.	.27	.76	.70	.70	.56	.76	.35	.64	.47	.56	.70	.76	.60	.60	-	87.9	69.7	44.3	85.2	73.1	75.7	66.9	65.5	63.5	36.4	21.4	59.[illegible]	72.6	53.7
16.	.29	.62	.67	.67	.60	.77	.44	.57	.67	.80	.67	.77	.83	.83	.56	-	73.4	41.0	92.4	76.6	78.9	67.5	71.0	58.8	29.0	25.0	55.4	78.4	45.8
17.	.44	.80	.71	.71	.67	.93	.36	.62	.54	.67	.71	.80	.86	.71	.70	.83	-	22.8	79.9	94.5	92.1	85.8	89.6	62.4	20.7	11.2	59.4	89.9	38.3
18.	.17	.67	.59	.59	.40	.79	.43	.53	.57	.67	.70	.78	.82	.71	.70	.67	.71	-	37.2	24.0	27.2	15.6	16.2	29.8	30.2	25.5	21.4	23.6	44.5
19.	.29	.77	.67	.67	.60	.77	.44	.57	.67	.80	.67	.77	.83	.67	.56	.80	.83	.67	-	83.[illegible]	85.6	74.[illegible]	78.3	58.1	29.6	17.7	55.2	83.5	45.0
20.	.22	.80	.71	.71	.67	.80	.54	.75	.54	.67	.71	.80	.86	.71	.70	.83	.86	.71	.83	-	95.8	34.9	38.7	60.3	21.1	6.3	57.9	92.4	37.5
21.	.17	.67	.59	.59	.40	.79	.28	.63	.57	.67	.70	.89	.82	.71	.70	.67	.71	.80	.67	.71	-	83.6	37.4	62.0	23.2	9.6	57.8	90.7	38.7
22.	.29	.77	.83	.83	.60	.77	.44	.43	.89	1.00	.67	.77	.83	.83	.56	.80	.67	.67	.80	.67	.67	-	94.6	48.5	16.1	1.2	50.[illegible]	57.2	28.1
23.	.25	.71	.62	.62	.54	.86	.40	.67	.80	.73	.75	.86	.92	.77	.63	.73	.77	.75	.73	.77	.75	.73	-	52.[illegible]	16.[illegible]	1.[illegible]	50.[illegible]	91.[illegible]	28.[illegible]
24.	.40	.88	.80	.80	.62	1.00	.33	.59	.67	.77	.78	.88	.93	.80	.76	.77	.93	.98	.77	.80	.78	.77	.86	-	46.[illegible]	44.5	57.4	54.4	66.6
25.	.44	.80	.71	.71	.67	.93	.36	.62	.73	.67	.71	.80	.86	.71	.70	.67	.86	.71	.67	.71	.71	.67	.92	.93	-	51.[illegible]	24.[illegible]	16.7	48.0
26.	.50	.57	.46	.46	.54	.71	.20	.53	.40	.36	.50	.57	.62	.46	.53	.54	.77	.50	.54	.62	.62	.36	.67	.71	.77	-	40.[illegible]	7.1	52.6
27.	.25	.71	.62	.62	.73	.71	.60	.80	.60	.54	.62	.71	.77	.62	.63	.73	.77	.62	.73	.92	.62	.54	.83	.71	.77	.67	-	51.7	54.7
28.	.33	.67	.54	.54	.67	.67	.60	.62	.75	.67	.57	.67	.73	.54	.47	.67	.73	.57	.89	.73	.57	.67	.80	.67	.73	.60	.80	-	30.2
29.	.22	.67	.61	.61	.48	.67	.30	.56	.40	.48	.77	.67	.61	.61	.54	.48	.61	.54	.48	.61	.69	.48	.54	.67	.61	.54	.54	.40	-

COMMUNITY COEFFICIENT (below diagonal); PERCENTAGE SIMILARITY (above diagonal)

TABLE VII

Matrix of percentage similarity and community coefficients for plant assemblages in coal-ball zones of Old Ben vertical section 4, in the Herrin (No.6) Coal

OLD BEN VERTICAL SECTION 4

DOMINANCE	COAL-BALL ZONES	1	2	3	4	5	6	7	8	9	10	11
Lepidophloios	1	-	22.3	45.0	41.6	20.5	82.4	2.9	39.2	42.1	28.3	47.0
Lepidodendron scleroticum	2	.73	-	37.8	17.6	31.8	19.3	22.3	29.2	45.3	16.4	17.5
Lepidophloios-Medullosa	3	.61	.62	-	78.5	63.8	50.9	48.3	71.7	61.1	65.1	52.9
Medullosa-Lepidophloios	4	.60	.61	.80	-	65.3	51.5	50.5	63.8	44.8	77.4	60.5
Medullosa-Psaronius	5	.75	.54	.62	.80	-	28.4	79.8	49.5	36.2	68.6	29.5
Lepidophloios	6	.73	.71	.75	.77	.73	-	12.6	54.7	52.0	38.1	61.8
Medullosa-Psaronius	7	.50	.36	.62	.80	.75	.54	-	35.6	21.6	67.4	13.7
Mixed dominance with Sigillaria	8	.57	.59	.74	.75	.57	.82	.57	-	64.5	50.2	64.0
Lepidodendron-Lepidophloios	9	.57	.71	.84	.75	.57	.82	.57	.80	-	40.0	69.8
Medullosa	10	.67	.67	.71	.71	.50	.80	.50	.78	.78	-	41.2
Lepidophloios-Lepidodendron dicentricum	11	.60	.62	.67	.83	.80	.77	.60	.62	.62	.57	-

PERCENTAGE SIMILARITY

COMMUNITY COEFFICIENT

Two regions of the VS 3–5 ordination merit special mention because of the unusual composition of the plant assemblages. Zones 2, 3, and 4 contain abundant *Paralycopodites brevifolius*. In most aspects these assemblages fall within the *Medullosa* "region" of the ordination. Zone 11, which is dominated by *Sigillaria* (32.9%), falls outside the three major regions and those that are transitional; in DCA ordinations it was an outlier on the first axis. Even when *Sigillaria* abundances are low, as in zone 8 of VS 4 (12%), the zones are compositionally outside the three common assemblages.

(2) Dominance-diversity patterns. Dominance-diversity curves representative of the major kinds of assemblages in VS 3–5 and VS 4 are illustrated in Figs.12–14. The curves allow comparison of biomass distribution among assemblages and provide an additional means for interpretation of ordination patterns.

Assemblages strongly dominated by *Lepidophloios hallii*, such as zone 23 of VS 3–5 (Fig.12) or zone 1 of VS 4 (Fig.14), are usually of low diversity. Little of the biomass is composed of plants other than *Lepidophloios*. Lower vascular plants with a homosporous free-sporing habit and ground cover plants are very rare or absent.

Transitional asssemblages, in which *Lepidophloios* is still dominant but at levels $< 70\%$, are represented by zones 16 and 12 of VS 3–5 (Fig.12). These assemblages have increased diversity, especially at the 1–10% biomass level, which includes a marked increase in *Psaronius* abundance. Other free-sporing and small, possibly ground-cover plants also occur.

Diaphorodendron scleroticum dominance is found in one or more zones of most Herrin

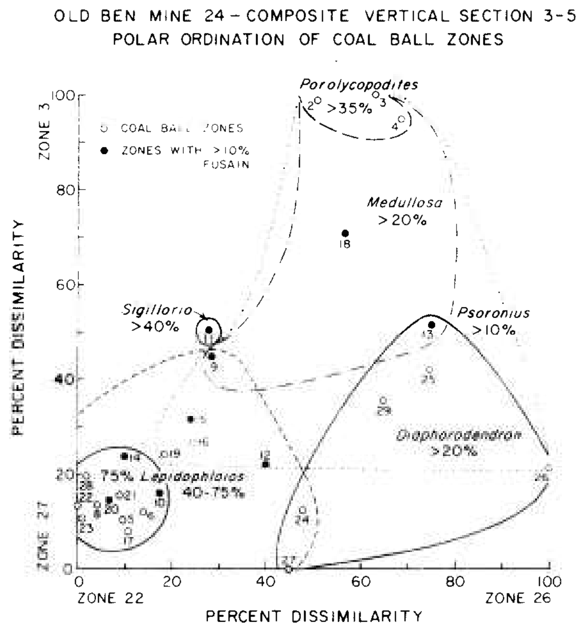

Fig.10. Indirect polar ordination of coal-ball zones (plant assemblages) in profile VS 3-5. Lines delimit the assemblages; the proportions of the major plants in each assemblage are shown within the respective "region" of the ordination. Based on root-free data.

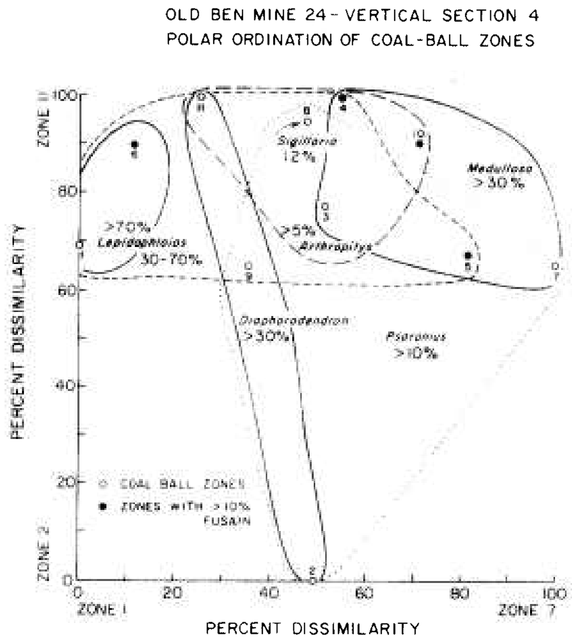

Fig.11. Indirect polar ordination of coal-ball zones (plant assemblages) in profile VS 4. Lines delimit the assemblages; the proportions of the major plants in each assemblage are shown within the respective "region" of the ordination. Based on root-free data.

profiles. High abundance frequently is distributed through several consecutive zones. Zone 25 of VS 3–5 (Fig.12) and zone 2 of VS 4 (Fig.14) illustrate *D. scleroticum* assemblages. *Diaphorodendron scleroticum* appears to have been one of the larger trees of the coal swamp (DiMichele and Phillips, 1985; Wnuk, 1985). It occurs with a variety of small ferns, pteridosperms, and sphenopsids, suggesting a structurally diverse assemblage in which most of the biomass was centered in *D. scleroticum*.

Diaphorodendron dicentricum occurs in most profile zones, but usually at $<10\%$ abundance. Where its abundance is $>10\%$, the assemblages usually have relatively high diversity. Few such zones occur in most profiles and they are most often in the upper third of the coal seam, frequently near the top of the profile. Zone 29 of VS 3–5 (Fig.13) and zone 8 of VS 4 (Fig.14) contain a large *D. dicentricum* element, are the most diverse of the respective profiles, and have the most equable biomass distributions. As a result of these factors, the dominance-diversity curves are broadly inflected. Such assemblages are complex associations of trees, shrubs, vines, and a large ground-cover component. Many of the important taxa in the assemblages, such as *Arthropitys, Sigillaria, Paralycopodites, Sutcliffia*, and numerous small ferns and pteridosperms, are generally less common in other zones of the coal-ball profiles.

Assemblages with $>20\%$ *Medullosa* are usually relatively diverse. They are commonly a mixture of small trees and shrubs. Zone 18 of VS 3–5 (Fig.13) and zone 10 of VS 4 (Fig.14) are *Medullosa*-dominated assemblages. *Medullosa* is a major subdominant in zone 2, VS 3–5 (Fig.12) and zone 8, VS 4 (Fig.14). Even assemblages such as that of zone 10, VS 4, which has the maximal abundance of *Medullosa*, retain the characteristic composition of mixed small trees and ground-cover found in other *Medullosa* assemblages.

Zone 2 of VS 3–5 (Fig.12) represents vegetation dominated by *Paralycopodites brevifolius*,

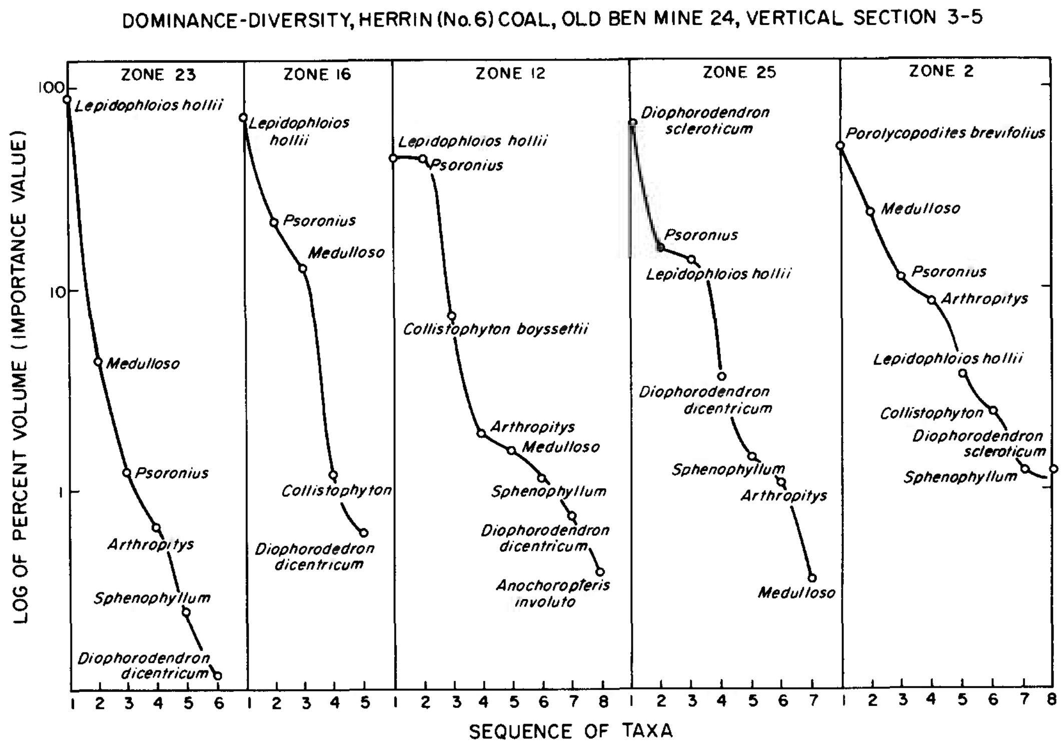

Fig.12. Dominance-diversity curves for representative plant assemblages from profile VS 3-5, based on root-free data.

found in three zones of VS 3–5. *Paralycopodites* dominates an association of small trees and shrubs that includes significant amounts of *Medullosa*. It is considered here to be a variant of the *Medullosa* assemblage.

Sigillaria is an uncommon component of assemblages from the Herrin. Zone 8, VS 3–5 (Fig.13) is the only major *Sigillaria* zone of the profile. Less common plants such as *Sutcliffia* and *Heterangium*, as well as *Arthropitys*, are often found in these relatively diverse assemblages. There are often many small plants and equable biomass distributions at low abundance levels.

(3) Fusain distribution. Zones with >10% fusain are noted on the ordinations. In VS 3–5, nine of the zones had >10% fusain, all from above the blue band (Fig.5). Of these nine zones, six have >10% *Medullosa* (aerial biomass), and pteridosperms (mostly *Medullosa*) comprise >40% of the fusain in the zones. The zones below the blue band with the highest fusain abundances in VS 3–5 were 2, 3, and 4, which had 7–9% fusain and >20% *Medullosa.*

In VS 3–5 the 12 zones with >10% *Medullosa* average 11.9% fusain (s.d. = 8.7%). *Lepidophloios* zones average 8.2% fusain (s.d. = 9.4%). Assemblages with >20% *Diaphorodendron* average 3.2% fusain. In VS 4 medullosan assemblages average 13.8% fusain, *Lepidophloios* assemblages average 8.6%, and *Diaphorodendron* assemblages average 5.0%.

Discussion

The Herrin Coal is the most widespread, thick coal from which coal-ball peats have been sampled extensively. Data from 17 profiles and 6 mines in southern Illinois and western Kentucky provide a broad perspective on the flora and its variability. The Herrin swamp was diverse both in the number of taxa and in the number of distinct assemblages these taxa comprised (Phillips and DiMichele, 1981; Phillips et al., 1985). This diversity is reflected

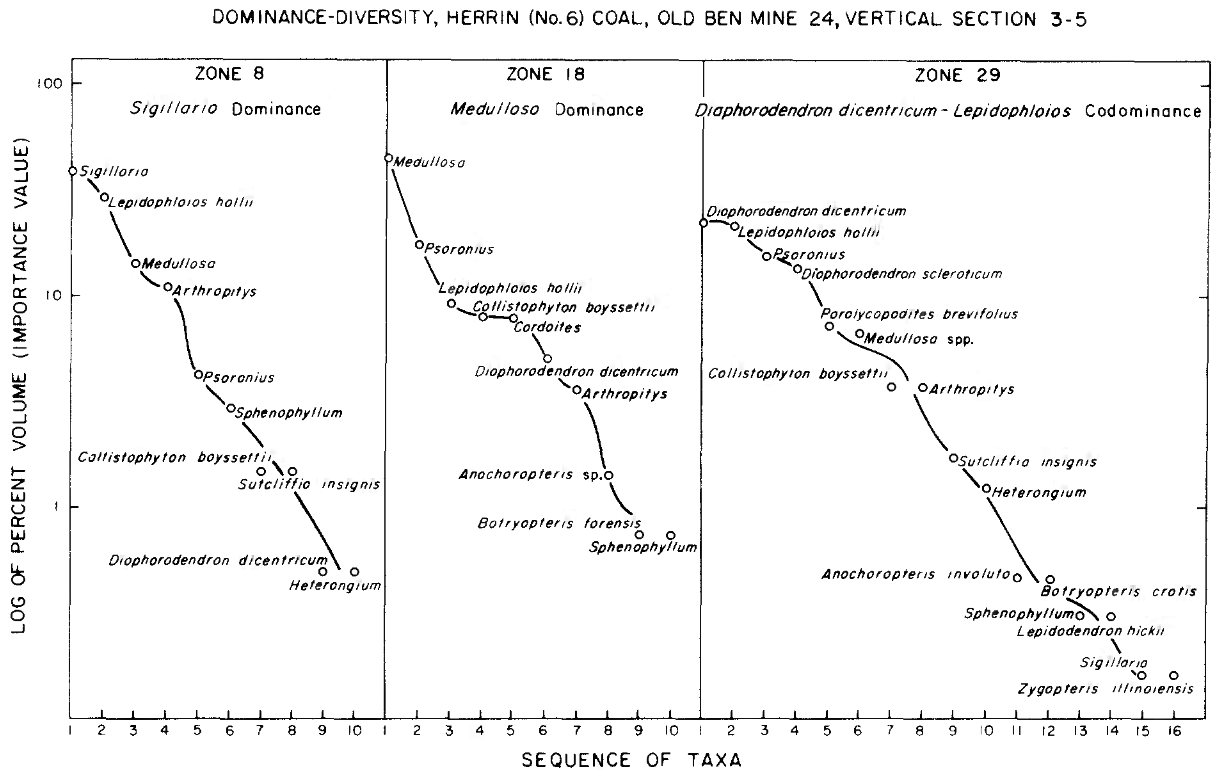

Fig.13. Dominance-diversity curves for representative plant assemblages from profile VS 3-5, based on root-free data.

spatially, among sites in the coal, and temporally, in profiles. In addition, there are recurrent vegetational patterns that appear to have occurred swampwide, such as the basal occurrence of associations with abundant medullosans, *Paralycopodites* and/or *Sigillaria* abundance near the blue band, and a rise in *Diaphorodendron* and tree ferns near the top of the seam.

The Old Ben samples are basically the same as those from other Herrin sites in plant and assemblage composition. The most notable distinctions are the somewhat lower diversity than some sites, and the large number of assemblages dominated by *Lepidophloios hallii*. The analyses of the Old Ben data sets are significant because the patterns that appear are relatively clear, suggesting that the natural patterns must have been quite conspicuous. Basic assemblages, those dominated by *Lepidophloios*, or rich in *Medullosa* or *Diaphorodendron*, also occur at other sites (Phillips et al., 1977; Phillips and DiMichele, 1981; Phillips et al., 1985). They appear to signal the predominant gradients, developed both locally and regionally within this swamp.

Plant associations and environments

Low-diversity, wet-site assemblages

Assemblages dominated by *Lepidophloios* are interpreted as indicators of standing water or very high water tables with saturated substrates. Such forests probably were very open canopied, since juvenile trees were unbranched (Andrews and Murdy, 1958) and even the mature trees appear to have been branched sparsely and clothed in short leaves (Chaloner and Meyer-Berthaud, 1983), permitting high light penetration. Diversity of the assemblages is very low, suggesting that few species were capable of growing under such conditions. The abundant species are either seed plants or plants with seed-like reproductive structures

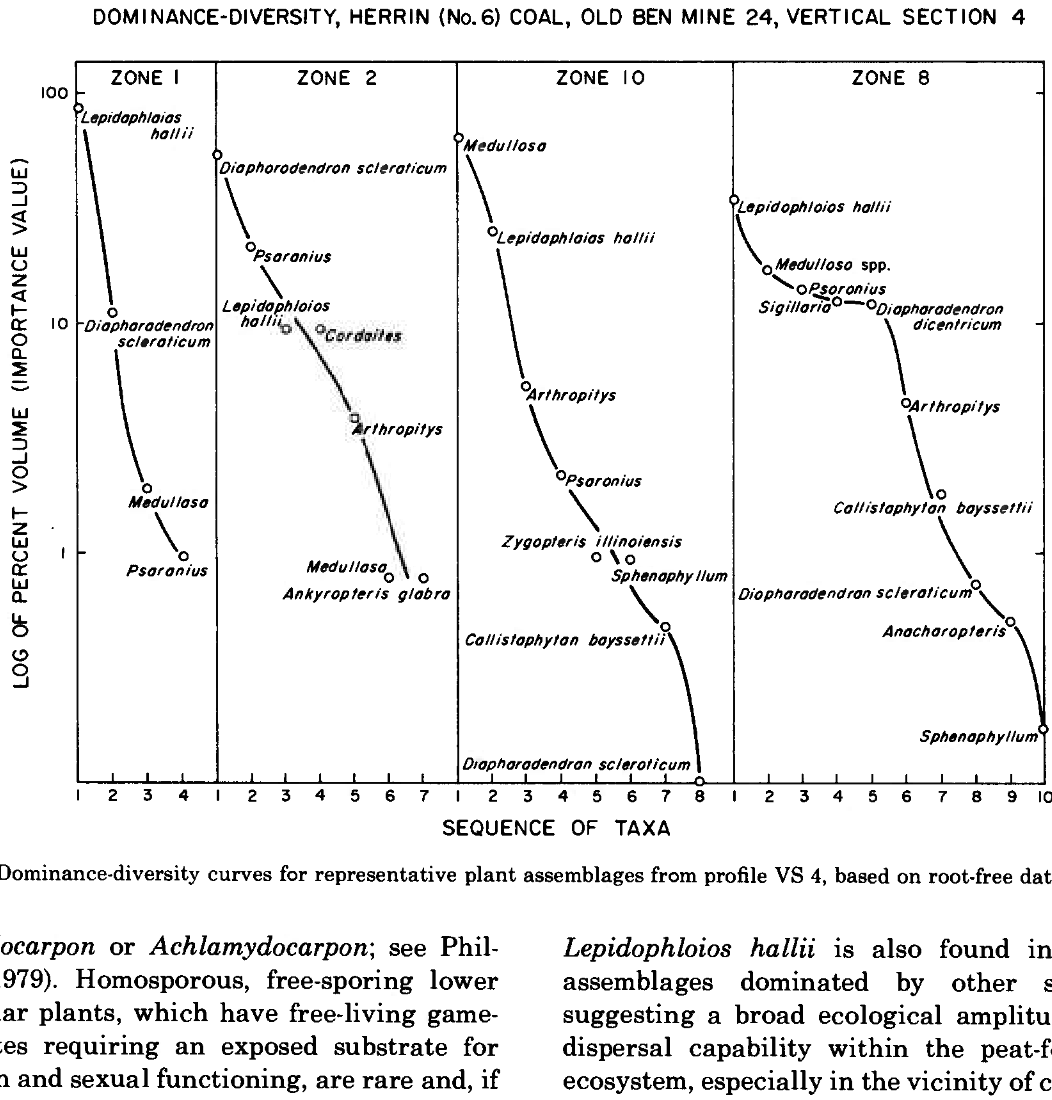

Fig.14. Dominance-diversity curves for representative plant assemblages from profile VS 4, based on root-free data.

(*Lepidocarpon* or *Achlamydocarpon*; see Phillips, 1979). Homosporous, free-sporing lower vascular plants, which have free-living gametophytes requiring an exposed substrate for growth and sexual functioning, are rare and, if present, occur in very low abundances (+/−1%) (Figs.12 and 14). This includes *Psaronius*, which is present at or above 10% biomass in most assemblages but sharply declines in abundance to around 1% or less as *Lepidophloios* abundance reaches 70–75%. Also rare or absent are ground cover or scrambling plants and presumed vines, mostly coenopterid ferns and pteridosperms.

The anatomy, habit and reproductive biology of *Lepidophloios hallii*, the dominant plant, are consistent with a habitat in which the water table is high (Phillips, 1979; DiMichele and Phillips, 1985). There were few other plants that could tolerate this kind of environment. *Lepidophloios hallii* is also found in many assemblages dominated by other species, suggesting a broad ecological amplitude and dispersal capability within the peat-forming ecosystem, especially in the vicinity of channel systems. The evidence from the succession of assemblages in profiles suggests that stands of *Lepidophloios* were self-replacing, persisting for considerable periods of time.

High-diversity, drier-site assemblages

Assemblages with >20% *Medullosa* were characteristic of habitats with large areas of exposed peat surface that were enriched in mineral matter and may have been subject to fire and severe peat decay. Patchy distribution, both within and among profiles, suggests discontinuous stands of low-canopied vegetation. These assemblages were relatively diverse taxonomically and structurally, including numerous small trees, ground cover, scramblers and vines. No coal-swamp species are characteristically excluded. Dominance-diversity curves frequently show mid-level inflection with several species exhibiting about 10% biomass.

Medullosa zones are common in proximity to the clastic seat earth and mineral partings in the coal (Phillips and DiMichele, 1981; Winston, 1986b). These mineral partings may have been derived from influx of clastics during flooding or from concentration during peat decay (Cecil et al., 1979). Such habitats may have been the most nutrient-rich of the coal swamp. The inferred drier, more nutrient-rich aspects of these assemblages are concordant with medullosan dominance in most clastic-substrate lowland habitats, including levees (Peppers and Pfefferkorn, 1970; Scott, 1978; Pfefferkorn and Thomson, 1982). There also is considerable species-similarity between the peat-swamp and clastic-substrate medullosan floras, a characteristic shared by few other coal-swamp plant groups (DiMichele et al., 1985).

Most of the fusain in Old Ben profiles occurs in medullosan-rich zones from mid-seam, in abundances not typical of the profile as a whole. If one were to suggest a fire-prone tree type in the coal swamps, *Medullosa* trees with their numerous resin-filled canals and thick cuticles would be prime candidates. The Old Ben profiles are the closest to the Walshville Channel that we have sampled and have a higher fusain content than those from sites farther from the channel. The greater inertinite abundance (versus liptinite dearth) pattern along the Walshville has been documented by Harvey and Dillon (1985) and would be consistent with wildfire sweeping along the exposed levee systems, and through the adjacent peat-swamp forest during periods of prolonged low water table.

Paralycopodites zones, a subset of *Medullosa* assemblages, occurred between the underclay and blue band as well as immediately above the blue band. They also are relatively high in fusain (8–9%) and, like *Medullosa* zones in general, are relatively diverse taxonomically and structurally. *Paralycopodites* usually is not an abundant plant in coal balls or clastic compressions (DiMichele, 1980), except in some thin coals (Hamlin Coal of eastern Kentucky; Secor Coal of Oklahoma) and splits of thicker coals (Springfield Coal of Indiana) (Phillips et al., 1985). Its abundance in association with clastic partings, and its general reproductive biology (DiMichele and Phillips, 1985) are consistent with a colonizer of disturbed, clastic-rich (transitional) peat substrates.

Diverse assemblages in moderately wet sites

There are two species of *Diaphorodendron* in the Herrin coal swamp with very different growth habits (DiMichele and Phillips, 1985; Wnuk, 1985) and distribution patterns. Moderate wetness in these sites is suggested by the low levels of fusain and mineral matter associated with these assemblages. *Diaphorodendron scleroticum* often is abundant in several consecutive zones (Figs.6 and 8), implying that stands existed on sites for extended periods at irregular intervals. The trees may have been "site occupiers" (DiMichele and Phillips, 1985). This is consistent with the occurrence of *D. scleroticum* in a variety of habitats. It was apparently one of the largest and longer-lived trees in the coal swamps. Diversity is usually moderate in *D. scleroticum* assemblages and other coal-swamp species may be present in varied orders of importance.

Diaphorodendron dicentricum appears to have been a colonizing species growing preferentially in sites of minor disturbance (DiMichele and Phillips, 1985). The species is widely distributed throughout profiles, occurring in most zones at 5% or less of the biomass (Figs.6 and 8). It reaches its maximal abundances (15–30%) in assemblages of high diversity, both taxonomic and structural, with numerous small trees, ground cover-ferns and vines, some of which are relatively rare.

Recurrent profile patterns

With the addition of the Old Ben profiles, a number of recurrent patterns in coal-ball peat profiles become evident in the Herrin coal swamp. Those previously reported are from southern Illinois and western Kentucky (Phillips et al., 1977; Phillips and DiMichele, 1981).

Beginning of the coal swamp

There may have been a protracted hiatus between the seat earth deposit and the onset of peat formation. However, coal-ball peats provide direct megafossil evidence on the early beginnings of the peat-forming phase. Profiles with coal-ball peats directly on the seat earth (Old Ben VS 5, Sahara VS 4, Delta VS 2) indicate that there was an abundance of medullosan pteridosperms in the basal-most peat-forming flora. These were part of a lycopod forest, which presumably accounted for the stigmarian rootlets in underclays and abundant roots in basal coal-ball peats. Among the basal coal-ball peat deposits, the kind of lycopod in profiles differs according to site: *Diaphorodendron scleroticum* at Old Ben, *Lepidophloios* at Sahara, and either *Lepidodendron hickii* or *Paralycopodites* in the Springfield Coal (Peabody Lynnville Mine, Indiana), all producers of stigmarian root systems.

A similar pattern has been described from the Bernice Basin (Anthracite Region) of Pennsylvania by Wnuk (1985) and Wnuk and Pfefferkorn (1984). They described a *Diaphorodendron (Lepidodendron)–Medullosa* forest from an organic shale immediately below the Mammoth Seam. Wnuk (pers. comm., 1986) continues to examine these exposures and has uncovered a patchy forest that also includes local stands of *Lepidophloios* and *Bothrodendron*. This may represent a deposit preserving transitional stages from clastic-rich to peat-forming swamp conditions. It is the same general age as the Herrin flora (Westphalian D) and has a flora that is similar in detail (Wnuk, 1985). In Illinois Basin underclays where floras other than stigmarian roots are preserved (Minshall, Seelyville and Colchester coals in the Middle Pennsylvanian), the predominant plants are medullosan pteridosperms; lycopods are absent. In underclays of the Lower Pennsylvanian Upper Cliff No.1 and No.2 coals in northern Alabama, Gastaldo (1986) uncovered in situ lycopod forests lacking a pteridosperm element. These differences in underclay floras suggest that a variety of transitional conditions may have preceded the onset of peat formation, and that medullosans and/or stigmarian lycopods were early components of that vegetation.

Up to the top of the blue band

The profile patterns between the underclay and the top of the blue band can be likened to the beginning of a coal swamp, its termination and a new beginning (on the blue band). Distinctive assemblages are those rich in *Paralycopodites* and/or *Sigillaria*. These occur abundantly somewhat below the blue band and on top of it in Old Ben VS 5, and between inferred "blue bands" in Sahara VS 4 and VS 5. A *Sigillaria*-rich zone occurs somewhat above the blue band in profiles from Old Ben, Sahara and other sites.

Middle seam patterns

The association of *Medullosa* assemblages with mineral-rich partings and higher fusain has been observed in numerous profiles from other mines; however, the cyclic repetition of these assemblages in Old Ben profiles is most distinctive. Profile 4 corresponds to the interval between zones 9 and 23 of VS 3–5 (Fig.3). Although exact zone to zone correlations can not be made, there is remarkable similarity in the patterns of change observed in the two profiles in the interval of overlap. This portion of the seam is the highest in macroscopic fusain and in petrologically-determined clastics and inertinite (Johnson, 1979). In this interval *Medullosa* reaches maximum abundance with the greatest number of abundance peaks. There is an almost cyclic alternation of zones of *Medullosa* dominance separated by several zones of lycopod dominance. Based on the measurements made at the coal face (Fig.3), the medullosan peaks do not correspond as lateral equivalents in the two profiles, 600 m apart. The similarity lies in the presence of distinctive medullosan peaks, the general inverse relationship of lycopods and pteridosperms, and the abundance of fusain-rich zones.

In general, other profiles from Old Ben that sample this interval also have very abundant pteridosperms and, in some cases, ferns. These observations suggest that the similarity between VS 3–5 and VS 4 is due to common ecological dynamics rather than exact co-occurrence of events in the two areas.

Upper seam patterns

The most notable patterns in the upper part of the seam are consecutive zones rich in *Diaphorodendron* and a subterminal zone or two of very abundant *Psaronius* tree ferns. The last is less distinct at Old Ben than at most other mines sampled (Phillips et al., 1977; Phillips and DiMichele, 1981). The similarity of such patterns probably is indicative of environmental trends that affect different parts of the swamp in overlapping or time-transgressive fashion rather than in swamp-wide time lines.

Summary

The Old Ben sites, as represented by VS 3–5 and VS 4, differ from other Herrin Coal assemblages in slightly lower diversity, the quantitatively greater abundance of *Lepidophloios* and the resultant thicker preserved coal-ball peat deposits. These distinctive characteristics could be attributed to a combination of earlier onset of peat formation, more stable high water table and differential subsidence in proximity to the Walshville. It appears that the Old Ben sites were close enough to the Walshville Channel for some parameters of plant growth and peat accumulation to be affected, but not close enough to result in markedly different vegetational patterns or patchy mosaics of vegetation, except perhaps with regard to medullosans and the mid-seam fusain-rich zones.

Large portions of the Herrin Coal are apparently similar in vegetational patterns and floras. In general, there appears to be as much variation in vegetation within and among samples from a given mine site as there is among samples from different mine sites. Within that pattern, however, regional differences have been detected with regard to proximity to the Walshville paleochannel. Palynological studies (Peppers in Phillips and Peppers, 1984) indicate a progressively increasing abundance of *Lycospora* (i.e., *Lepidophloios Lepidodendron* and *Paralycopodites*) nearer the channel, with higher tree-fern abundances in more central parts of the swamp.

Acknowledgements

We thank the Coal Section of the Illinois State Geological Survey and the Old Ben Coal Company for permission to carry out this study and for assistance in sampling. Geological Survey personnel Philip J. DeMaris, Robert Bauer, W. John Nelson, Heinz H. Damberger, and Richard A. Harvey provided geological information, and much discussion. The assistance of James F. Mahaffy, Daniel J. Guerra and Douglas Grierson is gratefully acknowledged. Figures were prepared by the School of Life Sciences Artist Service, University of Illinois. This research was supported in part by NSF Grant EAR 8313094 to T.L. Phillips.

References

Andrews, H.N. and Murdy, W.H., 1958. *Lepidophloios*, and ontogeny in arborescent lycopods. Am. J. Bot., 45: 552–560.

Bauer, R.A. and DeMaris, P.J., 1982. Geological investigations of roof and floor strata: Longwall demonstration, Old Ben Mine No.24. Ill. State Geol. Surv. Contract/Grant Rep., 1982-2, 49 pp.

Baxter, R.W. and Willhite, M.R., 1969. The morphology and anatomy of *Alethopteris lesquereuxi* Wagner. Univ. Kans. Sci. Bull., 48: 767–783.

Cecil, C.B., Stanton, R.W., Dulong, F.T. and Renton, J.J., 1979. Some geologic factors controlling mineral matter in coal. In: A.C Donaldson, M.W. Presley and J.J. Renton (Editors), Carboniferous Coal Shortcourse and Guidebook, AAPG Field Seminar, W. Va. Geol. Econ. Surv. Bull., B-37-3: 43–56.

Chaloner, W.G. and Meyer-Berthaud, B., 1983. Leaf and stem growth in the Lepidodendrales. Bot. J. Linn. Soc., 86: 135–148.

DeMaris, P.J., Bauer, R.A., Cahill, R.A. and Damberger, H.H., 1983. Geologic investigation of roof and floor strata: Longwall demonstration, Old Ben mine No.24 — prediction of coal balls in the Herrin Coal. Ill. State Geol. Surv. Contract/Grant Rep. 1983-2, 69 pp.

DiMichele, W.A., 1980. *Paralycopodites* Morey & Morey, from the Carboniferous of Euramerica — a reassessment of generic affinities and evolution of "*Lepidodendron*" *brevifolium* Williamson. Am. J. Bot., 67: 1466–1476.

DiMichele, W.A., 1985. *Diaphorodendron*, gen. nov., a segregate from *Lepidodendron* (Pennsylvanian age). Syst. Bot., 10: 453–458.

DiMichele, W.A. and Phillips, T.L., 1985. Arborescent lycopod reproduction and paleoecology in a coal-swamp environment of late Middle Pennsylvanian age (Herrin Coal, Illinois, U.S.A.). Rev. Palaeobot. Palynol., 44: 1–26.

DiMichele, W.A., Phillips, T.L. and Peppers, R.A., 1985. The influence of climate and depositional environment on the distribution and evolution of Pennsylvanian coal-swamp plants. In: B.H. Tiffney (Editor), Geological Factors and the Evolution of Plants. Yale Univ. Press, New Haven, Conn., pp.223–256.

Eble, C.F., Grady, W.C. and Gillespie, W.H., 1985. Palynologic and petrographic relationships in two Upper Kanawha Formation coalbeds of West Virginia (abstract). Geol. Soc. Am., Abstr. with Program, Southeast Section, 17: 90.

Esterle, J. and Ferm, J.C., 1986. Relationship between petrographic and chemical properties and coal seam geometry, Hance Seam, Breathitt Formation, southeastern Kentucky. Int. J. Coal Geol., 6: 199–214.

Gastaldo, R.A., 1986. Implications on the paleoecology of autochthonous lycopods in clastic sedimentary environments of the Early Pennsylvanian of Alabama. Palaeogeogr., Palaeoclimatol., Palaeoecol., 53: 191–212.

Gauch, H.G., 1982. Multivariate Analysis in Community Ecology. Cambridge Univ. Press, Cambridge, 298 pp.

Greig-Smith, P., 1983. Quantitative Plant Ecology. Univ. Calif. Press, Berkeley, Calif., 3rd ed., 359 pp.

Harvey, R.D. and Dillon, J.W., 1985. Maceral distributions in Illinois coals and their paleoenvironmental implications. Int. J. Coal Geol., 5: 141–165.

Johnson, P.R., 1979. Petrology and environments of deposition of the Herrin (No.6) Coal Member, Carbondale Formation, at the Old Ben Coal Company Mine No.24, Franklin County, Illinois. Thesis. Univ. Illinois, Urbana-Champaign, 169 pp.

Mahaffy, J.F., 1985. Profile patterns of coal and peat palynology in the Herrin (No.6) Coal Member, Carbondale Formation, Middle Pennsylvanian of southern Illinois. C.R. 9th Int. Congr. Carboniferous Stratigr. Geol., 5: 25–34.

Millay, M.A., 1979. Studies of Paleozoic marattialeans: a monograph of the American species of *Scolecopteris*. Palaeontographica, 169 B: 1–69.

Morgan, J., 1959. The morphology and anatomy of American species of the genus *Psaronius*. Ill. Biol. Monogr., 27: 1–108.

Oestry-Stidd, L.L., 1979. Anatomically-preserved *Neuropteris rarinervis* from American coal balls. J. Paleontol., 53: 37–53.

Peppers, R.A., 1970. Correlation and palynology of coals in the Carbondale and Spoon Formations (Pennsylvanian) of the northeastern part of the Illinois Basin. Ill. State Geol. Surv. Bull., 93, 173 pp.

Peppers, R.A. and Pfefferkorn, H.W., 1970. A comparison of floras of the Colchester (No.2) Coal and Francis Creek Shale. In: W.H. Smith, R.B. Nance, M.E. Hopkins, R.G. Johnson and C.W. Shabica (Editors), Depositional Environments in Parts of the Carbondale Formation — Western and Northern Illinois (Guidebook Ser., 8). Ill. State Geol. Surv., Champaign, pp.61–74.

Pfefferkorn, H.W. and Thomson, M.C., 1982. Changes in dominance patterns in Upper Carboniferous plant-fossil assemblages. Geology, 10: 641–644.

Phillips, T.L., 1979. Reproduction of heterosporous arborescent lycopods in the Mississippian–Pennsylvanian of Euramerica. Rev. Palaeobot. Palynol., 27: 239–289.

Phillips, T.L. and DiMichele, W.A., 1981. Paleoecology of Middle Pennsylvanian age coal swamps in southern Illinois/Herrin Coal Member at Sahara Mine No.6. In: K.J. Niklas (Editor), Paleobotany, Paleoecology and Evolution. Praeger, New York, N.Y., pp.231–284.

Phillips, T.L. and Peppers, R.A., 1984. Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence. Int. J. Coal Geol., 3: 205–255.

Phillips, T.L., Avcin, M.J. and Berggren, D., 1976. Fossil peat from the Illinois Basin (Educational Ser., 11). Ill. State Geol. Surv., Champaign, 39 pp.

Phillips, T.L., Kunz, A.B. and Mickish, D.J., 1977. Paleobotany of permineralized peat (coal balls) from the Herrin (No.6) Coal Member of the Illinois Basin. Geol. Soc. Am. Microform Publ., 7: 18–49.

Phillips, T.L., Peppers, R.A. and DiMichele, W.A., 1985. Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: environmental inferences. Int. J. Coal Geol., 5: 43–109.

Pielou, E.C., 1984. The Interpretation of Ecological Data. Wiley, New York, N.Y., 263 pp.

Rothwell, G.W., 1981. The Callistophytales (Pteridospermopsida): reproductively sophisticated Paleozoic gymnosperms. Rev. Palaeobot. Palynol., 32: 103–121.

Rothwell, G.W. and Warner, S., 1984. *Cordaixylon dumusum* n. sp. (Cordaitales). I. Vegetative structures. Bot. Gaz., 145: 275–291.

Schabilion, J.T. and Reihman, M.A., 1985. Anatomy of petrified *Neuropteris scheuchzeri* pinnules from the Middle Pennsylvanian of Iowa: a paleoecological interpretation. C.R. 9th Int. Congr. Carboniferous Stratigr. Geol., 5: 3–12.

Schopf, J.M., 1938. Spores from the Herrin (No.6) Coal bed in Illinois. Ill. State Geol. Surv., Rep. Invest., 50, 73 pp.

Schopf, J.M., 1939. Coal balls as an index to the constitution of coal. Trans. Ill. State Acad. Sci., 31: 187–189.

Scott, A.C., 1978. Sedimentological and ecological control of Westphalian B plant assemblages from west Yorkshire. Proc. Yorkshire Geol. Soc., 41: 461–508.

Shadle, G.L. and Stidd, B.M., 1975. The frond of *Heterangium*. Am. J. Bot., 62: 67–75.

Stidd, B.M., Oestry, L.L. and Phillips, T.L., 1975. On the frond of *Sutcliffia insignis* var. *tuberculata*. Rev. Palaeobot. Palynol., 20: 55–66.

Taylor, T.N., 1965. Paleozoic seed studies: a monograph of the American species of *Pachytesta*. Palaeontographica, 117 B: 1–46.

Thomas, B.A. and Watson, J., 1976. A rediscovered 114-foot *Lepidodendron* from Bolton, Lancashire. Geol. J., 11: 15–20.

Whittaker, R.H., 1975. Communities and Ecosystems. Macmillan, New York, N.Y., 385 pp.

Winslow, M.R., 1959. Upper Mississippian and Pennsylvanian megaspores and other plant microfossils from Illinois. Ill. State Geol. Surv. Bull., 86, 135 pp.

Winston, R.B., 1986a. Characteristic features and compaction of plant tissues traced from permineralized peat to coal in Pennsylvanian coals (Desmoinesian) from the Illinois Basin. Int. J. Coal Geol., 6: 21–41.

Winston, R.B., 1986b. Paleoecology and taphonomy of Middle Pennsylvanian-age coal-swamp plants: Herrin coal-ball peat and coal, Peabody Camp 11 Mine, Herrin Coal, western Kentucky. Thesis. Univ. Illinois, Urbana, 147 pp.

Wnuk, C., 1985. The ontogeny and paleoecology of *Lepidodendron rimosum* and *Lepidodendron bretonense* trees from the Middle Pennsylvanian of the Bernice Basin (Sullivan County, Pennsylvania). Palaeontographica, 195 B: 153–181.

Wnuk, C. and Pfefferkorn, H.W., 1984. The life habits and paleoecology of Middle Pennsylvanian Medullosan pteridosperms based on an in situ assemblage from the Bernice Basin (Sullivan County, Pennsylvania, U.S.A.). Rev. Palaeobot. Palynol., 41: 329–351.